OBSERVATIONS ON THE RESPIRATION OF AUSTRALORBIS GLABRATUS AND SOME OTHER AQUATIC SNAILS

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Trematode diseases are best eradicated, or at least reduced in their incidence, by interrupting the life cycle of the parasites in the intermediate hosts, that is, in the case of human infections, by instituting campaigns against the snails harboring the juvenile worms. This has been attempted to date by methods founded purely on empirical findings. It seems probable that a study of the physiology of the snails might yield important clues for the development of chemical means of control.

From a theoretical standpoint it appears likely that snails may be killed by the use of compounds interfering with the cellular respiratory mechanisms. As a preliminary to such work, a study was initiated of the respiration of some fresh water snails. We report in the present paper the results of our experiments on the normal aerobic respiratory physiology of *Australorbis glabratus,* the intermediate host of *Schistosoma mansoni* in the West Indies and South America. Included also are some data on the respiration of other snail species, most of them belonging to genera transmitting trematodes of man or lower animals.

Material and Methods

The following species of snails were employed:

1. Pulmonates

Planorbidae: Australorbis glabratus, laboratory reared from Venezuelan specimens; *Helisoma duryi,* in part specimens freshly collected at Kenilworth Gardens, Md., in part laboratory reared specimens derived from this stock; *Tropicorbis obstructus* and *T. donbilli,* both laboratory reared from specimens collected in Texas.

Lymnaeidae: Lymnaea stagnalis, collected from Mullet Lake, Michigan; *L. palustris* from Stemple Creek, Marin County, California; *L. obrussa* from a canal in the vicinity of Washington, D. C. These snails were used shortly after their arrival in Bethesda.

Physidae: Physa gyrina, in part specimens freshly collected at Kenilworth Gardens, Md., in part laboratory reared specimens derived from this stock; *Physa* sp. specimens freshly collected in a creek near Bethesda, Md., and laboratory reared specimens derived therefrom.

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2. Operculates

Amnicolidae: Amnicola limosa, collected in a canal near Washington, D. C.; *Oncomelania quadrasi,* laboratory reared specimens derived from snails collected in the Philippines; *O. nosophora,* used some weeks after having been received from Japan.

Viviparidae: Campeloma sp., used shortly after having been shipped from Douglas Lake, Michigan.

Melaniidae: Semisulcospira sp., laboratory reared specimens, derived from snails collected in the Philippines.

Pomatiopsidae: Pomatiopsis lapidaria, freshly collected specimens from Fairfax County, Virginia.

Pleuroceridae: Pachychilus sp., specimens collected in Guatemala and kept prior to the determinations for months in an aquarium.

Littorinidae: Littorina irrorata, recently collected from Wicomico River, Maryland.

All species, with the exception of *Littorina,* are fresh water species; *Littorina* occurs in brackish water.

With the exception of the very few cases in which entirely freshly collected specimens were used, the truly aquatic snails were kept in balanced aquaria in a room with a minimum temperature of 21° C. During the summer months the temperature rose to nearly 30° C. The snails were abundantly fed with lettuce leaves and fish food. From time to time some powdered calcium carbonate was added to the water. Those species (*Oncomelania, Pomatiopsis*) that lead in nature a semi-aquatic life were kept in aquaria simulating as best as possible their normal habitat (see Ward, Travis, and Rue, 1947, for details); their chief food consisted of leaf mold.

Before the snails were used for the actual determinations, the water adhering to the specimens was removed with filter paper; they were then weighed on an analytical balance to the nearest mg. The standard temperature used in all experiments, with the exception of those in which the temperature influence was studied, was 30° C. This temperature was slightly higher than that reached by the aquarium water during the summer months and was chosen in order to allow an adequate control of the water bath. This temperature was well tolerated by all species employed.

The respiratory medium was, during the first months of the study, filtered river water. Later on tap water was employed; this was allowed to stand for a minimum of 24 hours in the laboratory to permit the chlorine to evaporate. No difference in respiratory rate was noticed in either type of water.

The respiratory exchange was studied by means of Warburg manometers. The number of snails used for a single determination, the amount of water introduced into the flasks, the size of flasks employed, and the interval between readings varied, depending upon the size of the snails. Up to 16 specimens of the small species, or the juveniles of larger species, were used for each flask. The total capacity of these flasks was about 17 cc., and 2 cc. of water were used as respiratory medium. Of the largest species, single specimens were studied in flasks having a total capacity of about 120 cc.; in these cases 6 cc. of water served as medium. In this latter

case an equilibration period of one hour was necessary before the manometers could be closed while 20 minutes were sufficient when the smaller flasks were employed Depending upon the respiratory rate and the size of the flasks, readings were taken every 15 or 30 minutes for periods of two to four hours. The manometers were shaken with an amplitude of 4 cm. 100 times per minute. Most of the snails remained very quiet in the vessels; only the *Physa* species had a tendency to leave the water and to affix themselves to the sides of the flask.

In most cases the oxygen uptake alone was studied, the carbon dioxide being absorbed in the customary manner by means of 10 per cent KOH. In most series atmospheric air served as gas phase. In these series we were interested in the oxygen consumption of the snails in air saturated water, or, what amounts nearly to the same, that taken by pulmonates from the air itself. The question of the influence of varying oxygen tensions was studied only with *Australorbis glabratus*. In these experiments the gaseous atmosphere was changed by passing gases of known composition for a period of 20 minutes through the manometers. Details will be given in a later section.

The respiratory quotient was studied in some series of *Australorbis glabratus*. Since experience in other experiments had shown that the respiration of these snails stays fairly constant over long periods of time, a modification of Warburg's direct method was employed. The snails were first introduced into flasks containing no KOH and the change in manometer reading was followed for one hour or an hour and a half. The flasks were then removed from the manometers, KOH and filter paper were introduced into the center well and, after reequilibration to the temperature of the water bath, a second set of readings was taken for an equal period as above. The error due to possible changes in the respiratory rates is small since only such experiments were used in which the two sets of readings gave steady values. A few experiments in which either the first or the second set gave inconsistent readings were rejected. The snails used in these series were handled as little as possible; they were not dried or weighed in order to avoid injuries to the shell. This is a very important point since a pronounced carbon dioxide retention sets in very rapidly after the shell has been cracked. The readings taken in these series were calculated as mm^3. oxygen or carbon dioxide per one snail instead of being related to weight or surface area and the RQ was calculated from these values.

Results

1. Relations between size and respiratory rate

The snails varied considerably in size due both to species differences and to differences in age of specimens of one species. This gave an opportunity to study the relation between size and rate of oxygen consumption insofar as both inter- and intraspecific comparisons are concerned. The experiments summarized in this section were carried out from May to August; there was no indication that during this time seasonal variations in oxygen consumption occurred. The determinations were in a few cases carried out with freshly collected specimens; in most cases well fed aquarium snails were employed. This point is important. It will be shown in a later section that the respiratory rate of snails declines very rapidly during starvation. It was even repeatedly noted that determinations carried out on Mondays yielded somewhat lower values than during the remaining days of the week, the

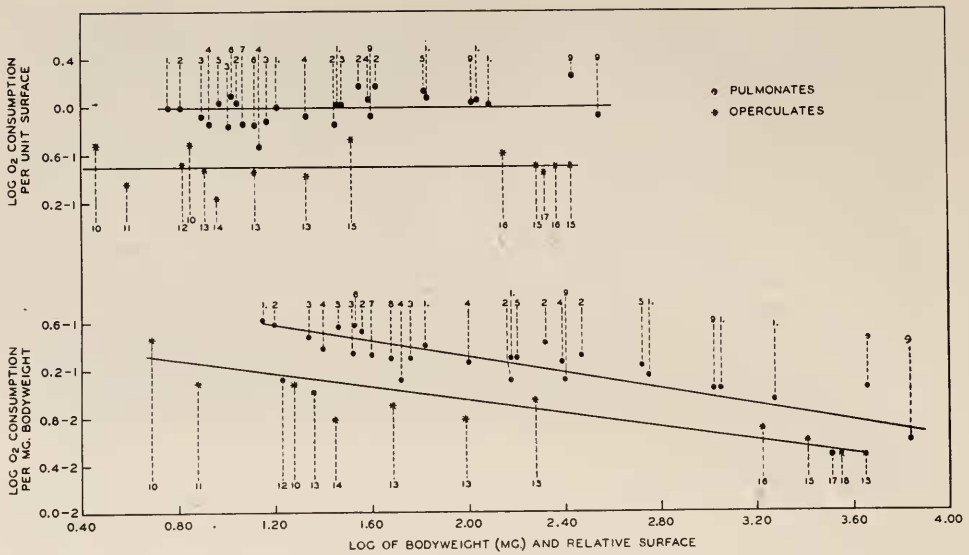

FIGURE 1. Relation between size and rate of oxygen consumption in various species of aquatic snails. Pulmonates: 1. *Australorbis glabratus*, 2. *Physa* sp., 3. *Physa gyrina*, 4. *Lymnaea palustris*, 5. *Helisoma duryi*, 6. *Lymnaea obrussa*, 7. *Tropicorbis donbilli*, 8. *Tropicorbis obstructus*, 9. *Lymnaea stagnalis*. Operculates: 10. *Amnicola limosa*, 11. *Oncomelania quadrasi*, 12. *Pomatiopsis lapidaria*, 13. *Semisulcospira* sp., 14. *Oncomelania nosophora*, 15. *Campeloma* sp., 16. *Pachychilus* sp., 17. *Littorina irrorata*.

TABLE 1

Respiration of Australorbis glabratus of various sizes at 30° C.
Mean values and, in parentheses, extremes

Number of experiments	Number of snails	Weight of single snail mg.	Mm.³ oxygen consumed by 1 snail in 1 hour	Relative surface	Ratios of		
					Weight	Oxygen consumption	Surface
6	40	14 (12, 16)	5.9 (5.4, 6.2)	5.8	1	1	1
6	24	66 (55, 76)	16.8 (14.0, 20.2)	16.3	4.7	2.8	2.8
6	12	153 (122, 201)	30.3 (25.1, 38.4)	28.6	11	5.1	4.9
6	24	564 (525, 601)	81 (60, 95)	68.3	40	14	12
6	6	1137 (1000, 1288)	110 (84, 156)	109	81	19	17
6	6	1903 (1646, 2220)	164 (105, 284)	154	136	28	27

reason being that the snails had more or less exhausted their food supply over the week end.

The data summarized in Figure 1 are average figures from 4 to 12 determinations each, in most cases from 6 determinations. The sizes of the snails are also average values. The data for *Australorbis glabratus* (Table 1) may serve to illustrate these points and the variability introduced by them.

The data, as shown in Figure 1, prove three facts. First, the respiratory rate of pulmonates was without exception higher than that of operculates when snails of equal weight were compared. Second, the respiratory rate of both pulmonates and operculates was inversely correlated to the size of the specimens when calculated on the basis of weight. The slope of the straight lines around which the values of the two groups fluctuated was almost identical, indicating that about the same percentage decline in respiratory rate with increasing weight occurred in both groups. Third, it is quite apparent that straight horizontal lines resulted if the respiratory rates were calculated on the basis of relative surface ($Weight^{2/3}$) rather than weight.

Several reasons may be responsible for the deviations from the average straight lines which in some cases were rather marked. Although we tried to use for the experiments summarized in this section only well fed snails, it is entirely possible that not all species were equally near an optimum diet. Another point is that only the soft parts of the snails are actively metabolizing while our data are based on the complex soft parts plus shell. It was for various reasons not possible to determine in each experiment the shell weight and therefore no attempt was made to correlate the oxygen figures to the weight of the soft parts. Sixteen determinations of the shell weight were carried out at various times during the present experiments on various species; it was found that it varied between 11.2 and 25.4 per cent. It is, of course, also possible that the metabolic rate of various species is inherently somewhat different, even if nutrition and all other factors were exactly equal. Despite these deviations, the trend of the curves is convincing.

It should be mentioned as especially noteworthy that small and large specimens of a given species followed rather closely the surface law, as shown in Table 1 on the example of *Australorbis glabratus*. This is remarkable since in many other organisms juvenile specimens show a higher rate of metabolism than would be expected from this relationship. It is pertinent to mention that the australorbids used for these experiments were all taken from a single aquarium and that the experiments with them were all carried out within two weeks. We were therefore dealing with an exceptionally uniform material insofar as food and physical environmental factors were concerned.

2. Influence of oxygen tension

The experiments on the influence of oxygen tension on the oxygen consumption were carried out with *Australorbis glabratus* specimens of two sizes, small snails weighing 30 to 40 mg. each and medium sized snails weighing 300 to 400 mg. each. Fully grown specimens could not be used because the gaseous atmosphere could not be changed conveniently in the large flasks that alone would accommodate them.

The rate of oxygen consumption of the snails was first established at the oxygen tension of atmospheric air for a period of 1¾ to 2 hours with readings taken at 15 minute intervals. A gas mixture of known oxygen tension was then passed for 20

minutes through the flasks. After the manometers had been closed, the rate of oxygen consumption at the experimental tension was followed for two hours. The temperature was in all experiments 30° C. Twelve experiments were carried out for each of the two groups at each of the four experimental oxygen tensions, and each time new snails were employed.

The summary of all experiments (Table 2) indicates that the reactions of both size groups to changes in oxygen tension were very nearly identical. It is probably justifiable to assume that fully grown specimens would have reacted in an essentially

TABLE 2

Influence of oxygen tension on the oxygen consumption of Australorbis glabratus at 30° C. Mean values and, in parentheses, extremes

Series	O_2 consumption at 160 mm. Hg. tension mm.³/1 gm./1 hr.	Experimental O_2 tension mm. Hg.	O_2 consumption at experimental tension	
			Mm.³/1 gm./1 hr.	Per cent of 160 mm. value
A	296 (254, 318)	760	288 (250, 334)	98±8.0
B	140 (101, 177)	760	144 (97, 190)	104±3.1
A	255 (226, 270)	38	205 (186, 221)	81±2.0
B	161 (122, 187)	38	138 (99, 178)	86±2.3
A	311 (249, 416)	13	260 (234, 279)	85±3.2
B	163 (129, 183)	13	156 (110, 204)	95±4.1
A	246 (187, 310)	5	29.6 (8.2, 49.2)	12±0.4
B	177 (147, 262)	5	12.5 (3.8, 17.3)	7±0.7

Series A: Snails weighing 30 to 40 mg. each.
Series B: Snails weighing 300 to 400 mg. each.

identical manner. On the whole, there was little indication that the oxygen consumption was markedly influenced by changes in tension between 760 and 13 mm. Somewhere below this latter tension the consumption began to fall off rapidly; at a tension of 5 mm. only a small fraction of the normal amount was consumed. The data obtained prove conclusively that *Australorbis glabratus* belongs to the group of invertebrates capable of maintaining a more or less uniform rate of oxygen consumption over a wide range of tensions.

3. Influence of temperature

The influence of temperature on the rate of oxygen consumption of *Australorbis glabratus* was investigated in the range of 0.3 to 41° C. The experiments were carried out with fairly small snails, the individual specimen weighing from 40 to 90 mg. Six snails were introduced into each flask and 12 experiments were conducted for each experimental temperature. New snails were used for each experiment. The respiratory rate of every lot was first established at our standard temperature of 30° C., four readings being taken at 15 minute intervals. The manometers were then transferred to a second water bath regulated to the intended experimental temperature. After equilibration the respiration was followed for a two hour period with readings taken at 15 or 30 minute intervals at the higher and lower temperatures respectively. The manometers were then transferred back to the original 30° C. water bath and a new set of readings was taken at 15 minute intervals in order to test whether during this recovery period the original level of oxygen consumption would again be reached.

The absolute values obtained in the various series during the initial 30° C. period varied somewhat, due probably to the differences in size between snails of the

TABLE 3

Influence of temperature on the oxygen consumption of Australorbis glabratus, averages and, in parentheses, extremes

Initial oxygen consumption at 30° C. mm.³ O_2/1 gm./1 hr.	Experimental temperature °C.	Oxygen consumption at experimental temperature		Oxygen consumption at 30° C. following experimental temperature			
				First hour		Second hour	
		Mm.³ O_2/1 gm./1 hr.	Per cent of initial value	Mm.³ O_2/1 gm./1 hr.	Per cent of initial value	Mm.³ O_2/1 gm./1 hr.	Per cent of initial value
151 (119, 186)	0.3	6.6 (3.7, 10.0)	4.3±0.25	58 (39, 74)	39±2.9	111 (73, 151)	75±6.9
222 (169, 260)	5.0	15.2 (11.8, 17.4)	6.9±0.34	131 (101, 162)	60±4.0	225 (185, 290)	102±4.7
208 (155, 256)	10.0	21.3 (16.7, 27.9)	10.2±0.16	204 (166, 253)	98±1.9		
184 (136, 224)	14.8	48.3 (40.0, 54.3)	27±1.3	178 (167, 196)	99±5.0	175 (150, 222)	97±4.9
179 (141, 234)	19.7	88 (76, 96)	50±2.2	185 (158, 214)	105±3.9		
175 (134, 200)	24.7	115 (94, 140)	67±3.5	168 (145, 188)	97±2.9		
193 (139, 228)	37.0	281 (226, 358)	148±7.0	193 (138, 260)	99±3.8		
225 (190, 282)	41.0	158 (111, 221)	71±3.7	152 (86, 248)	68±7.2		

various batches and to small differences in their nutritional state. These differences do not, however, interfere with an evaluation of the experiments since the figures found during exposure to the experimental temperatures and those obtained during the recovery period could be expressed in per cent of the initial value, thus eliminating any influence of these variations.

The oxygen consumption of the snails (Table 3) increased in the range 0.3° to 37° C. At 41° C., however, the animals were definitely damaged. Their respiratory rate decreased, and it did not come back to the original level during the recovery period. After the end of the recovery period, the snails were kept in beakers over night at room temperature and it was found that all were dead the following morning. The lowest temperature employed, 0.3° C., was also damaging. The respiratory rate increased only slowly after the snails had been transferred back to 30° C., and, after being kept over night at room temperature, about half the snails were dead. All other temperatures were well tolerated and the respiration returned during the recovery period to the pre-experimental value.

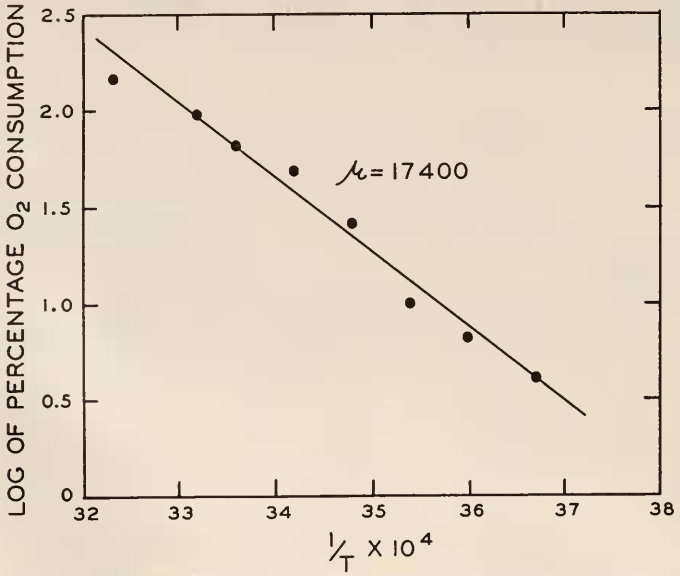

FIGURE 2. Temperature relationships of the oxygen consumption of *Australorbis glabratus* in the range 0.3° to 37° C. expressed according to Arrhenius' equation.

Using the percentage oxygen figures, the temperature relationship was then calculated according to Arrhenius' equation (Fig. 2) for the range 0.3° to 37° C. A single straight line was obtained and the μ value of 17,400 is entirely within the normal range.

Upon projection of the percentage figures on Krogh's (1914) normal curve a very satisfactory agreement to this curve was obtained (Fig. 3). Krogh's curve has been established only for the range 0° to 29° C. The points obtained in the present investigation beyond this range show an excellent fit to an extension of this curve. It would seem possible that this extension may have the same general applicability as the original curve.

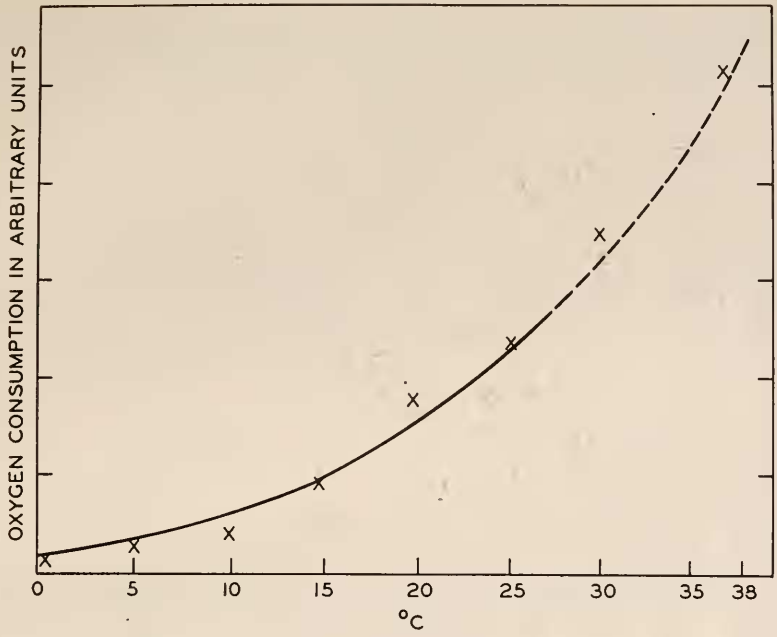

FIGURE 3. Projection of the percentage oxygen figures of *Australorbis glabratus,* taken from Table 3, on Krogh's normal curve and extension of this curve to 37° C.

4. Influence of starvation

The influence of starvation on the rate of oxygen consumption was studied with *Australorbis glabratus, Helisoma duryi, Physa* sp., and *Physa gyrina.* Of the three former species six groups of two snails each were employed while six groups of four snails each were used of *P. gyrina.* The snails of each species were selected as to uniformity in size. Each group was kept in a beaker with about 200 cc. water which was changed at frequent intervals and which was aerated by a slow stream of air bubbling through the water. The experiments were carried out during the summer months, the beakers being kept in a room without temperature control. The water temperature was, however, checked daily. It varied between 21.0° and 29.5° C.; the average temperature was about 27° C. The rate of oxygen consumption was determined for each group at the start of the starvation period, and after designated periods of starvation; the temperature during the actual determinations was 30° C.

The snails were weighed before each determination. The average loss in weight towards the end of the experiments was 18 per cent of the original weight in the case of *Physa* sp., 13 per cent both in *Australorbis glabratus* and *Physa gyrina,* and only 3 per cent in *Helisoma duryi.* Why this latter species lost relatively so little weight is not clear; it was the species that resisted starvation longest. Because this loss in weight would mask to a certain extent the decrease in metabolic level, if the oxygen values would have been calculated on the basis of the weight the organisms had on a specified day, the values are expressed in mm^3. oxygen/1 snail/1 hour.

Figure 4 shows that the various series ended after three to seven weeks starvation. When one snail out of a group died, the group was discarded and the whole series was completed when one of the snails of the last remaining group had died. Obviously then, our figures do not indicate the upper limit of starvation that the

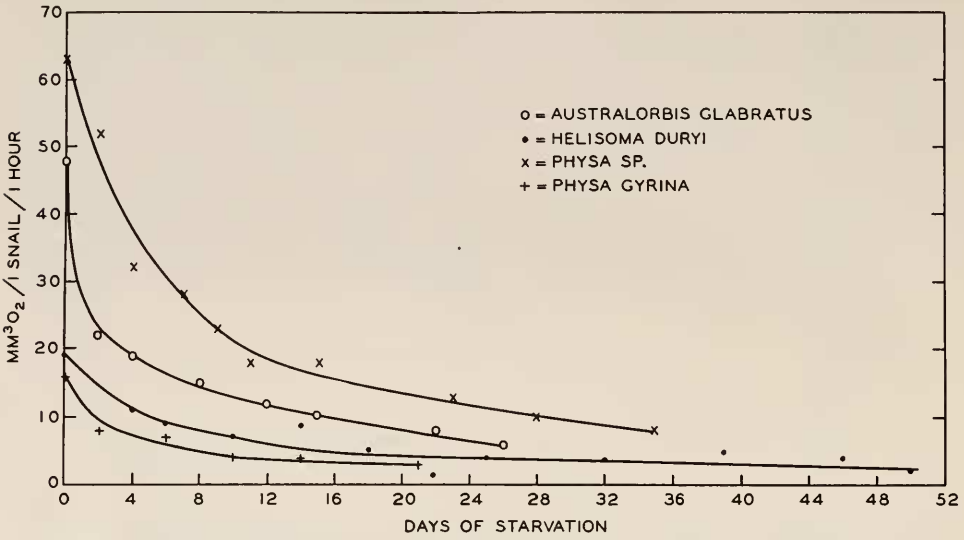

FIGURE 4. Influence of starvation on the rate of oxygen consumption of four species of pulmonate snails, absolute figures.

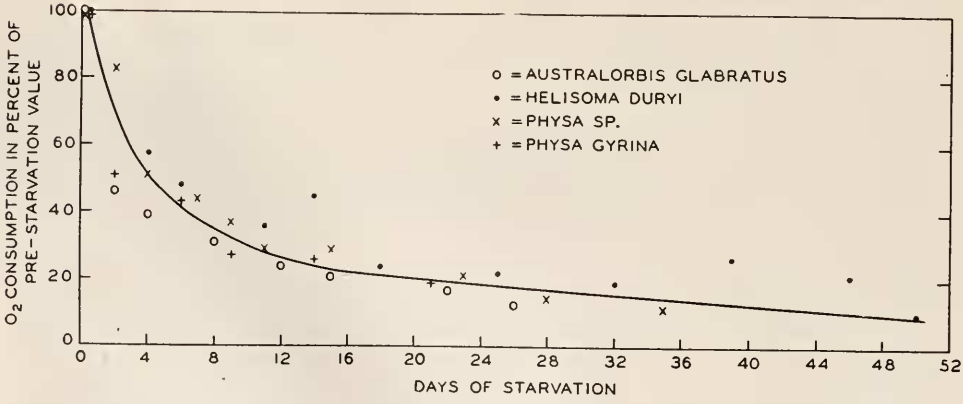

FIGURE 5. Influence of starvation on the rate of oxygen consumption of four species of pulmonate snails, percentage figures.

various species can endure at the temperature prevailing in our experiments. We are even hesitant to assume that all our snails died of actual starvation; the unavoidable repeated handling may well have hastened the end of one or the other specimen.

It is obvious (Fig. 4) that in all four species the rate of oxygen consumption declined sharply during the initial stages of starvation. Later the decline was much

less marked, but no completely steady level was reached. In order to test whether the influence of starvation was noticeably different in the various species, the starvation values were then calculated in per cent of the initial values. This eliminated the differences in the absolute amounts due to the various sizes of the snails belonging to the different species. Figure 5 shows that the values thus obtained fit fairly well to a single curve; really large deviations occurred only during the first days of starvation. On the whole it is evident that the effect of progressive starvation was quite similar in the four species studied.

The respiratory quotient was studied only in the case of *Australorbis glabratus*. The snails were kept in these experiments in a room with an average temperature of approximately 25° C. but the actual RQ determinations were carried out at our standard temperature of 30° C. The points shown on Figure 6 are mean values of from five to 14 determinations each.

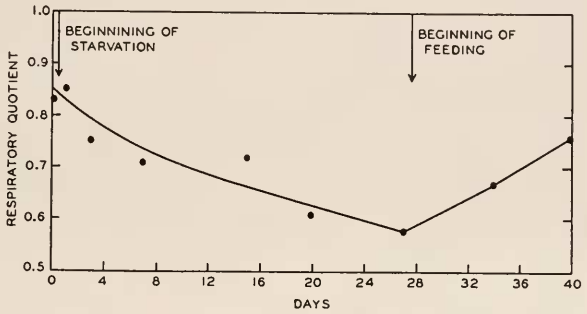

FIGURE 6. Respiratory quotient of *Australorbis glabratus* under the influence of starvation and subsequent feeding.

The respiratory quotient of well fed snails was around 0.85; the values found during the progressive stages of starvation fluctuated around the curve shown in Figure 6. A progressive lowering is evident and after three to four weeks starvation the surprisingly low value of 0.6 was reached. After 27 days inanition the snails were again fed and the respiratory quotient determined after one and two weeks feeding. It did rise during this period markedly but failed to reach the pre-starvation level.

DISCUSSION

The present investigation has shown that aquatic pulmonate snails have consistently a higher rate of oxygen consumption than operculates of the same size. A definite reason for this difference could not be adduced; it is an illustration of the well known fact that animals with different organization frequently have different metabolic levels.

In both groups the respiratory rate was inversely correlated to the weight of the specimens, but remained more or less constant if referred to relative surface. This relationship held true both in intraspecific and interspecific comparisons and was especially close in the former case. The question of the relationships between body size and metabolic rate has recently been reviewed by von Buddenbrock (1939), Kleiber (1947), and Zeuthen (1947). While the surface law applies rather

closely in the case of most vertebrates, the matter is more complex in invertebrates, or when the animal kingdom as a whole is considered. Large deviations are especially apparent in the largest and smallest organisms for which data are available. Insofar as molluscs specifically are concerned, Weinland (1918) found a positive correlation between surface and respiratory rate in *Anodonta,* while Liebsch (1928) denies such a relationship in terrestrial snails; he found a positive correlation between weight and respiratory rate. It should be pointed out, however, that the nutritional state of his snails was not uniform and that the size range of his specimens was appreciably smaller than that employed by us. An inspection of our data (Fig. 1) shows that within limited size ranges lines apparently showing a constancy of weight/O_2 relationship could be drawn but that the over all picture is distinctly against the validity of such a procedure. In view of the present results, it would be interesting to reinvestigate the terrestrial snails on a broader basis; it would be rather remarkable if they differed so fundamentally from the aquatic species.

It is true, however, that differences between terrestrial and aquatic snails have been reported also in other respects. It is thus a well established fact that the former show a pronounced dependency of their oxygen consumption on the oxygen tension (Thunberg, 1905; Dahr, 1927; Fischer, 1931; Harnisch, 1932) while many marine snails do not (Moore, Edie, Whitley, and Dakin, 1912; Raffy, 1933). *Australorbis glabratus* belongs, according to the present investigation, to this latter group. This, unquestionably, is due to the haemoglobin in its blood. Although the oxygen dissociation curve of the *Australorbis* haemoglobin has not yet been studied, it can be presumed to resemble that of the closely related *Planorbis.* The oxygen affinities of the latter's haemoglobin make it especially suited to procure oxygen at low tensions (Leitch, 1916; Borden, 1931).

The fact that *Australorbis* can hold its oxygen consumption at a normal level even at relatively low tensions may have a bearing on control measures. The application of some chemicals to snail infested waters results in the snails' burrowing into the mud and so escaping the direct action of the poison (W. H. Wright, personal communication). Although it is not known whether *Australorbis glabratus* specifically reacts in this way, it must be expected that snails with similar respiratory characteristics would not be easily killed by asphyxiation simply by being driven into oxygen-poor surroundings. Under very low oxygen tensions, it is true, the oxygen consumption is markedly lowered. It must be remembered, however, that snails in general are endowed with fairly well developed anaerobic functions (summary of the literature in von Brand, 1946).

The temperature relationships of *Australorbis glabratus* correspond to those commonly found in other invertebrates. The range of temperatures tolerated at least for the short periods employed in the experiments was rather wide. The variations in metabolic level encountered in this range may well have to be taken into consideration in control measures directed against this schistosomiasis-carrying species. Due to the lower metabolic level the snails will consume less food at lower temperatures than at higher ones. A poison, therefore, that acts via the alimentary canal may have to be kept longer at a given concentration in the cooler headwaters of a stream than in the warmer lower regions in order to insure that it reaches adequate concentrations within the tissues of the snail. It should be noted in this connection that according to Luttermoser (1947) in Venezuela at least "the only

workable method for eradicating the snails was to eliminate them in the headwaters and to destroy them progressively downstream." Very likely, however, the temperature range in schistosomiasis-endangered river systems will not be quite so broad as the extremes employed in our laboratory experiments.

The influence of starvation on the oxygen consumption of *Australorbis glabratus, Helisoma duryi, Physa gyrina,* and *Physa* sp. was pronounced and quite similar in the four species. A progressive lowering in metabolic level occurred until the snails finally died. No steady rate of oxygen consumption was reached, the snails resembling in this respect starving warm-blooded animals (Krogh, 1916).

The respiratory quotient of *Australorbis glabratus* sank during starvation from an initial value of 0.85 to the surprisingly low level of around 0.6. Even lower values have been observed by Bellion (1909) in *Helix* and by Liebsch (1928) in several species of terrestrial pulmonates. *Helix* was studied towards the end of hibernation, that is, after having starved for a long time; Liebsch's specimens were probably at least semi-starving. The interpretation of the respiratory quotients of animals having calcareous shells is notoriously difficult; the following interpretation can therefore be only tentative. In view of the fact that the occurrence of glycogen has been demonstrated in *Australorbis glabratus* (von Brand and Files, 1947), it does appear probable that the relatively high RQ of well fed snails is due to the utilization of this polysaccharide. The glycogen reserve does not seem to last for a long time; soon values typical for fat and protein consumption are reached. The very low values found in the last stages may indicate either the new formation of carbohydrate from protein or, possibly, fat, or they may be due to carbon dioxide retention. The data at hand do not permit a decision between these possibilities.

The respiratory quotient of australorbids fed again after a starvation period of four weeks rose but failed to reach in two weeks the original level. Before starvation, the snails had been kept in a balanced aquarium; during and after the inanition period they were kept isolated in pairs in beakers. It is possible that they had in the aquarium some accessory food material at their disposal that was lacking in the beakers. But it is equally possible that during the recovery period a certain amount of carbon dioxide retention took place in connection with restitution processes on the shell. We gained at least in some cases the impression that the shells became brittle during protracted periods of starvation but we do not have quantitative data proving this point and emphasize that we do not consider it as more than a possibility. It may be mentioned that during hibernation, which of course corresponds to a starvation period, movements of inorganic substances between soft parts and shell likely occur in the case of *Helix* (von Brand, 1931).

Summary

1. A study of the rate of oxygen consumption of nine species of pulmonate snails and eight species of operculate snails showed that the pulmonates had consistently a higher metabolic level than the operculates if specimens of equal weight were compared.

2. In both groups, the intensity of oxygen consumption decreased with increasing size of the specimens if referred to unit weight, but remained about constant if referred to relative surface. The oxygen/surface relationship held true both in inter- and intra-specific comparisons and was especially close in the latter case.

3. *Australorbis glabratus* was able to maintain an approximately steady rate of oxygen consumption over a wide range of oxygen tensions.

4. The oxygen consumption of *Australorbis glabratus* increased with rising temperature in the range of 0.3 to 37° C., but 41° C. was lethal. The temperature relationship calculated according to Arrhenius' equation gave within the tolerated temperature range a straight line. A good fit to Krogh's normal curve was also obtained and an extension of this curve to a higher temperature range than used by Krogh is presented.

5. The intensity of the oxygen consumption of four species of pulmonate snails sank during protracted starvation first rapidly and later on slowly without reaching a steady level. The respiratory quotient of *Australorbis glabratus* sank during inanition to very low levels and rose only slowly after feeding was begun again.

6. The possible implications of some of the studied factors on snail control measures are briefly discussed.

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